Long-Term Memory and Aging

A Cognitive Neuroscience Perspective

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There is little doubt that with age, long-term memory function declines. Countless behavioral studies have revealed significant differences in memory for lists of words (Smith, 1977), text (Dixon et al., 1982), and visual details (Park & Puglisi, 1985; Park, Puglisi, & Latz, 1982), faces (Bartlett et al., 1989), abstract visual materials (Smith et al., 1990), and even television news (Friesen & Park, 1999). Although it is clear that memory decreases with age, there are a number of different views regarding the mechanisms underlying these age-related declines. Advances in neuroimaging have provided unprecedented opportunity to explore the neural underpinnings of behavioral theories of age-related memory decline and have resulted in new insights and neurally based theories accounting for memory phenomena associated with aging. In this chapter, we provide an updated view of what is known about aging and memory, integrating behaviorally based research with more recent neurally based findings.

Dominant views of causes of age-related declines in memory are varied in the cognitive aging literature. One broad theory is that there is a decline in processing resources, limiting the ability to encode and retrieve information. The clearest and perhaps earliest instantiation of this theory was presented by Craik and Byrd (1982). They argued that observed age-related declines in memory were caused by decreased "mental energy" or processing resource that limited the ability of older adults to engage in self-initiated processing. Later theorists have suggested that empirical measurement of processing resource could be represented by speed of information processing (Salthouse, 1994, 1996) or working memory capacity (Park et al., 1996, 2002; Salthouse et al., 1988; Salthouse & Babcock, 1991), both of which decline with age. Studies have conclusively demonstrated that both speed of processing and working memory mediate most, if not all, age-related variance in long-term memory (Park et al., 1996, 2002; Salthouse & Babcock, 1991), demonstrating the utility of these constructs for understanding long-term memory.

In contrast to resource-based theories of speed and working memory, inhibition theory (Hasher & Zacks, 1988; Zacks & Hasher, 1997) suggests that older adults are less effective at gating or selecting information. Hence, they have less capacity available for effective encoding and retrieval of material, resulting in a long-term memory deficit. Other views of causes of memory decline with age include poor source memory (Johnson, Hashtroudi, & Lindsey, 1993), for which decreased ability to remember the context or source in which information is presented limits accurate recall of material with age.

Rather than focusing on age-related differences in difficulty recalling specific components of a memory, such as context, Jacoby and colleagues (Jennings & Jacoby, 1993, 1997) suggested that there is an overall age impairment in recollection. They have argued that to understand age differences in memory, it is important to differentiate between memory processes that rely on explicit memory and memory based on feelings of familiarity. Jennings and Jacoby demonstrated convincingly that young adults rely on veridical explicit memory traces for memory performance, with some contributions from feelings of familiarity. In contrast, older adults' memory performance is dominated by automatically activated feelings of familiarity rather than explicit traces, resulting in degraded accuracy of their recall relative to young adults.

The connection of these cognitive theories of age-related decline in memory to neural function is one goal of this chapter, as is explicating new views of the aging memory that have resulted from neuroimaging studies. At the outset, it is important to note that the clarity and relative simplicity of behavioral theories are not mirrored in the neuroimaging literature. There are literally an infinite number of activation and deactivation patterns possible to be associated with memory function in a complex, three-dimensional structure like the brain. Older adults may activate less, more, or even different neural structures to perform a memory task than young adults do (see Park et al., 2001; Cabeza, 2002; and chapter 2 of this volume for a more extended discussion of this issue). Further complicating interpretation of neural differences associated with aging on memory tasks are volumetric decreases in neural tissue that occur with age, with less particularly marked in the frontal cortex (Raz, 2000; Raz et al., 1996). Nevertheless, despite these complications, neuroimaging studies have provided much insight into an understanding of aging and memory.

There are certain issues about memory that neuroimaging data are uniquely suited to answer. Behavioral measures of memory cannot ascertain if observed age differences result from strategy differences or mental effort exerted at encoding, as a result of differences in retrieval processes, or both. Neural activity, however, can be independently measured at encoding and retrieval, providing a unique window into processes that separately occur at these stages of memory.

In addition, neuroimaging allows a direct mapping of levels of activation in different brain sites to memory performance. Recall that Craik and Byrd (1982) suggested that decreased mental energy was the basis for age-related decline, which might lead one to expect consistently decreasing neural activation with age. However, neuroimaging studies suggest a different mapping. For example, Cabeza (2002) has argued that memory encoding and retrieval in older adults are often accompanied
by increased activation relative to young in the frontal cortex. Specifically, he suggested that hemispheric-specific activation in young adults may be reorganized in older adults, particularly in those with early-onset Alzheimer’s disease. In other studies, this pattern of activation has been linked to the left and right hemispheres. As will be discussed, this pattern is consistent with the findings of previous studies and may indicate that cognitive processes in older adults are altered. However, the exact nature of these changes is still not fully understood. Further, the use of imaging techniques is limited by the complex interactions between the brain and the rest of the body. For example, the use of functional magnetic resonance imaging (fMRI) in older adults is limited due to the increased noise in the signal. Despite these limitations, fMRI studies have provided valuable insights into the brain's functional organization and have been used to investigate the changes that occur with aging.

A second problem with studying memory loss in older adults is that older adults often perform worse than young individuals. This is true in both verbal and non-verbal memory tasks. However, older adults do not always show age-related declines in memory. Some studies have found that older adults actually perform better than young adults on memory tasks. This is known as the “age-related memory effect.” This effect may be due to the fact that older adults are more likely to use strategic memory strategies, such as rehearsal, than young adults. However, it is not clear whether this effect is due to differences in cognitive processing or differences in motivation. In this chapter, we will examine the factors that influence memory performance and the implications of these findings for our understanding of memory and aging.
ences in plasticity, strategy, and process is quite remarkable. These data are not only creating significant constraints for behavioral theories of aging, but are resulting in a tremendously fresh focus on new learning and strategy changes with age in the behavioral literature.

We also focus our review on neural activations in both frontal and hippocampal areas. Theorizing that aging impacts of cognitive resources can be deployed flexibly by the frontal cortex, so that inconsistencies could result from strategy differences between subjects, particularly in memory tasks for which there may be multiple routes to successful encoding and retrieval. Furthermore, shrinkage of the prefrontal cortex and localization of compensatory sites could vary because of individual differences with aging, leading to difficulty interpreting group results.

In addition to focusing on the role of the frontal cortex in age differences in long-term memory, we also focus considerable attention on the hippocampus and related medial temporal structures, which are critically important for encoding and associating novel information into memory (Stern et al., 1996; Brewster et al., 1996; Wagner et al., 1998; Cohen et al., 1999). We propose that, with age, memory function is characterized by (1) decreased engagement of the hippocampus and other medial temporal areas; (2) relatively reliable age differences in left frontal activations, with some studies showing heightened activity and others less activity with age; (3) bilateral activity in the frontal cortex in older adults when young adults show unilateral activity. Similar to the confusing picture with respect to the frontal activations, age-associated bilateral activity sometimes results from increases in activation of the nondominant hemisphere by older adults (Cabeza, Graff, et al., 1997; Bäckman et al., 1997; Madden et al., 1997; D’Esposito et al., 2002; Rosen et al., 2002); in the older adult in the dominant hemisphere activated by the young (Logan et al., 2002; Strother et al., 2002). Whether bilateral activations (as well as relatively equivalent levels of activation in the old in the left and right prefrontal cortex (bilaterality), whereas young adults showed a focal, unilateral pattern of left frontal activations. The compensation hypothesis emerged from these data as Cabeza, Graff, et al. suggested that the observed bilaterality in the old could be caused by a compensatory recruitment of the right hemisphere as a result of inadequate activations in the left hemisphere.

The findings from these two initial, pioneering studies prove to be reliable, and the observations from these seminal studies continue to be the basis for much theorizing. The notion that the aging brain was not simply characterized by linear declines in activity was provocative and convergent with the theorizing and findings of Heffer-Lorenzo and colleagues (2000) on working memory. In an astonishingly short period of time, it became nearly obligatory for behavioral researchers reporting on memory function to integrate their behavioral findings with these seminal studies and with later neuroimaging work on aging and memory. Other early findings were suggestive of the engagement of qualitatively different neural networks to perform encoding tasks. Madden et al. (1997) studied intentional word encoding and reported that regression analyses of reaction times and regional cerebral blood flow indicated that left prefrontal activations predicted young but not older adults’ reaction times. Rather, for old adults, reaction times predicted left
The behavioral literature on the impact of sleep on memory is extensive. Several studies have shown that sleep is necessary for the consolidation of new memories. 

In a recent study, participants were divided into two groups: one group slept for 7 hours, and the other group slept for 4 hours. The results showed that the group that slept for 7 hours had significantly better memory recall than the group that slept for 4 hours. This suggests that sleep is crucial for the consolidation of new memories.

Moreover, the brain's ability to process and retain new information is affected by sleep. During sleep, the brain goes through a cycle of REM (rapid eye movement) and slow-wave sleep. In REM sleep, the brain is highly active and prepares for the next day's learning. In slow-wave sleep, the brain is more relaxed and consolidates the day's memories.

In conclusion, sleep plays a crucial role in memory consolidation. It is essential for the brain to process and retain new information. Therefore, promoting healthy sleep habits can improve memory and cognitive performance.
The data on levels of processing provide an inconsistent picture of encoding differences in neural activations as a function of age. Generally, the studies found consistent evidence for bilaterality in older adults, but it was often caused by decreased activation of the left frontal cortex relative to young adults (rather than increased engagement beyond the level of younger adults, so if it harder but not impossible) to make a compensation argument for this pattern than for a pattern in which activation increases above the level of young adults. Moreover, the data suggest increased activation in left frontal areas in mildly demented subjects might be taken as evidence of a disinhibition or decreased selectivity rather than for the compensation argument, but it could also plausibly be that subjects with the poorest neural function showed the most activation, thus arguing that the pattern is supportive of compensation.

We believe that to reconcile whether deep encoding is characterized by more or less left frontal recruitment and whether the frontal recruitment is compensatory, it is important to demonstrate encoding conditions within subjects that increase or decrease engagement of left frontal areas in older adults. Relating such changes in frontal engagement to performance as well as to individual differences of subjects will bring much clarity to the issue of deep processing, aging, and left frontal activation.

The results of level-of-processing manipulations on medial temporal function are somewhat clearer. Of the three studies that examined activations in medial temporal areas, all reported some age differences in the role of the hippocampus in intentional versus deep incidental comparisons (Grady et al., 1999), deep versus shallow incidental encoding comparisons (Daseelah, Veltman, Romboots, Raajmakers et al., 2003), or correlations of the hippocampus with behavior (Grady et al., 2002).

Finally, a methodological point worth noting is that, in a number of the studies (Steebins et al., 2002; Daseelah, Veltman, Romboots, Raajmakers et al., 2003), memory was not assessed or not reported. Future studies should include memory outcome measures because, without behavioral measures, it is difficult to interpret activation patterns, and actually, if there are no memory measures, it is uncertain whether these encoding conditions should be considered as memory studies. In closing this section, we should also note that the reports of the effects of deep versus intentional processing on memory in older adults in the behavioral literature are quite variable (see Kausler, 1990, for a review). Although the level-of-processing effect has proven to be one of the most reliable and integrative for the study of human memory, models that address changes in the quantity or engagement of processing resources with age have not been the most informative in understanding aging memory (e.g., Craik, 1996; Hasher & Zacks, 1979; see reviews in Hasher & Zacks, 1988, and Park, 2000). Hence, we suspect that confusion about engagement of neural resources will not be resolved by studying the depth of processing manipulations.

Differences in Encoding of Remembered Items

Since the seminal Grady et al. article on memory and aging was published in 1995, techniques for measuring neural signal have evolved. Event-related fMRI allows accurate recording of signal with a temporal resolution of as little as 2 s for whole...
brain coverage. Event-related designs are particularly useful for the study of memory because neural events associated with successful versus unsuccessful encoding of individual stimuli can be measured.

Using fMRI, Wagner et al. (1998) recorded event-related signal during encoding of words. Then, based on out-of-the-scanner recognition performance for the words, they sorted successfully encoded items (those recognized with high confidence) from those forgotten (those that were missed). The findings revealed that subjects were more likely to engage the parahippocampal gyrus for remembered compared to forgotten items, a finding also reported for pictures by Brewer et al. (1998).

There are three studies to date in the aging literature (Morcom et al., 2003; Daselaar, Veltman, Rombouts, Laerzen, et al., 2003; Gutches et al., in press) that have used the subsequent memory paradigm to examine the neural signal at encoding associated with items that are remembered. These studies are particularly important as they may potentially provide insight into the difficult arguments regarding the relationship between heightened activation levels and compensation in older adults. If greater activation, it would be expected to see more bilaterality and greater activation above perhaps young baseline levels for remembered versus forgotten items. Thus far, the findings are somewhat variable, with two of the three studies showing some evidence for decreased medial temporal activation for remembered items in old individuals and a mixed picture for frontal areas.

Morcom et al. (2003) studied word memory using an incidental, deep-processing task. When forgotten items were subitems, young and old adults showed equivalent levels of activation in the left inferior frontal cortex, supporting the findings of Logan et al. (2002) for deep processing. Old individuals showed enhanced activity for forgotten items compared to remembered items and, on query of frontal cortex in a regions-of-interest analysis, more bilateral anterior prefrontal activation for remembered items compared to young. Whether this additional recruitment is compensatory or merely decreased selectivity of encoding is not clear, as old adults cannot be determined from the pattern of findings. In addition, both groups showed more hippocampal engagement for remembered items, although young individuals showed more activation of the left anterior inferior temporal cortex for remembered compared to forgotten items than old adults.

Daselaar, Veltman, Rombouts, Laerzen, et al. (2003) conducted a similar study, but due to an inadequate number of misses they compared remembered items to baseline rather than to subjects. Unlike Morcom et al. (2003), they observed equivalent amounts of lateralization between old and young individuals. The most interesting finding was related to hippocampal activation and occurred when older adults were divided into high-performing and low-performing memory groups based on recognition performance. The old-low individuals showed less medial temporal activation for remembered items than either old-high or young adults.

Finally, Gutches et al. (in press) examined memory for pictures in an incidental, deep-processing task. They reported more parahippocampal activation in young adults compared to old for remembered items, even when subjects were not divided into high and low performers. They also found significantly more recruitment of the left frontal cortex in old adults compared to young adults for remembered items. Given that pictures generally induce bilateral prefrontal activations (Kelley et al., 1998), the older adults' increased recruitment of the left prefrontal cortex above the level of young adults suggests a selective activation that is potentially compensatory. The subsequent memory paradigm is a potentially rich tool that, with sufficient n's and varied encoding conditions, may permit disentangling functional from dysfunctional neural signal. At present, the findings have not yielded the clarity that one would hope for, but we believe that event-related designs that can separate the neural signal associated with remembered items from forgotten items offer a powerful tool that will yield a better understanding of memory function in late adulthood, particularly when individual differences to cognitive performance are examined, as demonstrated by Daselaar, Veltman, Rombouts, Laerzen, et al. (2003). Sorting remembered from forgotten items provides specificity at the level of process, and differentiating subjects based on cognitive performance provides specificity at the level of ability.

We should note that two of the three studies provided some evidence for decreased medial temporal activation with age for remembered items. The hippocampus is the primary structure that deteriorates with Alzheimer's disease. Alzheimer's disease is a ubiquitous disorder in later years; about 40% of older adults aged 85 years and older have frank Alzheimer's disease (Raskoll et al., 2002; Launer et al., 1999). Given the disorder's long and slow progression, it is very plausible that decreased hippocampal activations in older adults may reflect early-stage Alzheimer's disease. If this is the case, apparent age differences in this region would be driven by a subset of subjects. The differences between old-high and old-low individuals found by Daselaar, Veltman, Rombouts, Laerzen, et al. (2003) are consistent with such an explanation.

Nonverbal Stimuli

The study of meaningful pictures is an ideal medium for understanding age differences in neural circuits and potentially compensatory neural processes in older adults because it is often possible to equate performance between old and young adults on picture memory tasks (Park, Puglisi, & Smith, 1986; Park et al., 1988; Smith et al., 1990), permitting a clear interpretation of different patterns of neural signal. Moreover, the encoding of relational elements within meaningful scenes in particularly demanding of the hippocampus (Cohen et al., 1999; Stern et al., 1996), providing a strong medium for assessing medial temporal as well as frontal function in older adults. There are several studies that have used pictorial stimuli with older adults, and overall they present a strong picture of decreased hippocampal function with age, with a more variable pattern for frontal activations.

Gandy et al. (1999) directly contrasted pictorial and verbal memory in young and old adults, presenting line drawings of objects as well as words for study. Generally, older adults showed similar patterns of neural circuitry, but decreased activation relative to young in frontal and medial temporal areas. The exception was a contrast between deep and shallow processing for pictures, for which older and younger adults showed relatively similar levels of activation increases in left prefrontal and medial temporal regions. It is important to note that these were line drawings of simple objects and probably made low demands on relational processes in the hippocampus.
Divided Attention of Scanning

Movements that occur while encoding and recognition processes occur against a background of distraction. Movements that occur primarily during shallow encoding and recognition processes rather than deep encoding (Gollub, et al., 1995).

Differences in visual search strategies and strategies for encoding chunks of information may result in differences in scanning patterns. These differences in scanning patterns may be more pronounced for young adults than for older adults. Older adults show lower activation levels than young for the enhanced stimulus. Older adults, because they have been trained to use more strategic approaches during encoding processes that occur when distracting tasks or information are present, show lower activation levels than young adults.

Dual-Task Performance

Dual-task performance is another way in which encoding and recognition processes occur against a background of distraction. Dual-task performance is often used as a proxy for encoding and recognition processes. Dual-task performance is often used as a proxy for encoding and recognition processes, and it is used to assess how well people can perform multiple tasks at the same time. Hence, an understanding of how encoding processes interact with recognition processes is an important step in understanding how encoding and recognition processes occur against a background of distraction.

There is a large body of literature on age differences in dual-task performance. In general, older adults show lower performance than young adults when performing dual tasks. However, the differences in dual-task performance between young and older adults are not as pronounced as those observed in single-task performance. This is because older adults are more likely to use strategies that allow them to perform the two tasks simultaneously. However, older adults may still be slower than young adults when performing dual tasks.

Other researchers have investigated the effects of aging on encoding and recognition processes in other ways. For example, some studies have found that older adults show lower activation levels than young adults during encoding processes. However, these differences are not as pronounced as those observed in single-task performance. This may be because older adults are more likely to use strategies that allow them to perform the two tasks simultaneously. However, older adults may still be slower than young adults when performing dual tasks.

In summary, dual-task performance is a way in which encoding and recognition processes occur against a background of distraction. Dual-task performance is often used as a proxy for encoding and recognition processes. Dual-task performance is often used as a proxy for encoding and recognition processes, and it is used to assess how well people can perform multiple tasks at the same time. Hence, an understanding of how encoding processes interact with recognition processes is an important step in understanding how encoding and recognition processes occur against a background of distraction.
study, Grady et al. (1995) found that young individuals showed right prefrontal activity, as well as right parietal and bilateral occipital activations, when recognizing encoded faces, confirming the JERKA model. Older adults also showed right prefrontal activations, but no significant activations in the other regions exhibited by the young. In addition, they reported a correlation of .94 between the activity in the frontal cortex and right hippocampal activity for young adults, but no relationship for older adults (r = .02).

These findings were replicated in a later study (Grady et al., 2002) and are suggestive of different retrieval networks with age, with young adults relying more on hippocampal circuitry than old adults. Madden et al. (1999) also confirmed the pattern of engagement of different networks for recognition in old compared to young individuals. In this study, regression analyses of reaction time to regional cerebral blood flow suggested that memory retrieval networks encompass more regions (specifically in posterior cortex) in elderly adults. Thus, these studies suggested that retrieval may involve a qualitatively different neural network in old compared to young people.

Difficulty and Effort Manipulations at Retrieval

Behaviorally, performance differences as a function of age become larger as tasks require more directed retrieval (Light, 1991). For example, age differences are larger for explicit compared to implicit memory (LeVoe & Light, 1994; Park & Shaw, 1992) and for recall compared to recognition (Craik & McDowd, 1987; Rabinowitz, 1984, 1986; Schofield & Robertson, 1986). Blackman et al. (1997) measured neural activations in a PET scanner in young and old adults under different memory conditions. In the explicit condition, subjects were instructed to complete letter stems with studied words and with the first word that came to mind that completed the letter stems in the implicit condition. During explicit retrieval, both young and old adults showed increased activation of right prefrontal cortex when contrasted with implicit performance. Young adults showed unique activations as well in Wernicke's area and the left cerebellum for explicit retrieval, but the overall pattern was one of similar engagement of frontal systems for retrieval in young and old adults.

Cabeza, Grady, et al. (1997) conducted, using PET, one of the few studies contrasting verbal recall with recognition. They found increased activation in the right frontal cortex with age, resulting in a pattern of bilateral activation for old and a more unilateral pattern for young adults. In addition, differences in activation patterns between recall and recognition were larger for young compared to old adults, suggesting less differentiation of neural activity in old individuals as a function of retrieval condition.

Schacter et al. (1996) varied how well subjects learned words at encoding for young and old adults. Using PET to image retrieval for the words, Schacter et al. found old and young individuals had equivalent hippocampal activations, and that these activations increased for better encoded words. Prefrontal activations, however, differed, with young adults showing typical increases in the anterior frontal cortex during retrieval, whereas older adults showed a more posterior pattern of frontal recruitment. This again supports the conclusion that older adults engage different networks at retrieval than young adults, although it is not clear whether the differential engagement reflects strategic differences or neural reorganization.

Anderson et al. (2000) manipulated divided attention at retrieval in young and old adults following the encoding of word pairs. They reported that divided attention had little effect at retrieval on either old or young adults, reflecting the obligatory nature of the retrieval process.

Finally, Daelelaar, Veilman, Rombouts, Lauwereins, et al. (2003) presented a pattern of findings that potentially account for inconsistencies in activation patterns among studies. They studied retrieval following semantic encoding of words and reported a pattern of decreased frontal activity in older adults. A split of high and low performers within the old group, however, revealed that low-performing elderly showed more prefrontal activations than young adults, whereas high-performing elderly showed the least, suggesting that disparate findings can be reconciled via the study of individual differences.

In general, neural patterns associated with episodic retrieval showed less dramatic differences between old and young than encoding studies. Moreover, all studies noted frontal decreases, with considerably less evidence for hippocampal differences than is true in the encoding literature. Finally, there was considerable evidence for engagement of different networks with age, but whether these reflect neural reorganization or strategy differences is not clear from the present studies.

Recognition of Autobiographical Memories

Magram and Fein (2003) examined the role of personally relevant information in recognition for young and old adults. They collected information from each subject regarding memory for specific autobiographical and public events prior to an experimental session and designed stimuli that were unique to the individual selected for presentation in an fMRI study. An intriguing pattern of age-related changes in hippocampal activations occurred. They found that elderly adults recruited the hippocampal bilaterally for autobiographical event retrieval trials, whereas young adults showed left-lateralized activations. Unlike the encoding studies reviewed, this study suggested that conditions do exist in which elderly adults activate the hippocampus more than young. Personally relevant or emotional information is likely part of an elaborative semantic network and may be less fragile than purely experimental episodic information, thus eliciting robust hippocampal activations. Understanding whether rich, elaborated memories show different activation patterns than less-elaborated traces, at both encoding and retrieval, is an important issue for future research.

Context and Memory

There is a large body of behavioral literature on the benefits of contextual materials at encoding. In fact, some theorists argued that poor memory for contextual or source information is a fundamental mechanism accounting for poor memory in older adults (Johnson, Hashbrouck, & Lindsay, 1993). Findings indicated that older adults show
larger differences for context memory than for item memory (Park & Puglisi, 1985; Park, Puglisi, & Lint, 1982; Spencer & Raz, 1995) and have problems in binding target to context (Chalfonte & Johnson, 1996). Other behavioral work has focused on the potentially supportive role of context at encoding and retrieval and the working memory requirements of utilizing context. In paired associate tasks, when a target is unrelated to context and requires active integration and engagement of working memory, age differences are larger than when the context automatically activates an associaton through semantic relationships (Park et al., 1998; Smith et al., 1990, 1998).

At this point, there are only a few studies that have examined age differences in neural activations underlying contextual manipulations. Otsuka et al. (2001) studied age differences in encoded and unrelated pictures. Both young and old adults showed increased left prefrontal activation for unrelated pictures compared to the control condition, reflecting the increased processing demands of utilizing the unrelated pictures as cues. At the same time, older adults showed less activation than young adults in right occipitotemporal cortex, suggesting that they were less likely to encode the visuospatial features of the stimuli. No significant frontal activation were observed for young or old adults in the related-item condition, suggesting the relatively automatic encoding of related items: another possible cause is that the power in this study was low, even by imaging standards, with only seven subjects in each age group.

Two other studies of aging and context focused on retrieval of contextual information. First, Cabeza et al. (2000) used PET and studied item and item memory associated with the encoding of words. They reported that young adults showed increased activation in the right prefrontal cortex for order information compared to item information, whereas older adults did not, exhibiting less engagement of frontal areas in old compared to young individuals. This finding is consistent with reports of more impaired memory for context in older individuals (Spencer & Raz, 1995). It is important to note as well that a pattern of activation suggestive of compensation for order information was observed in older adults. They showed weaker activations in the right prefrontal cortex compared to young adults, but greater activation in left prefrontal areas.

In a later study, Cabeza et al. (2002) presented subjects with words that were spoken aloud or presented visually and then measured neural activation at recognition for items and source. They again found that young adults showed lateralized activations in the right prefrontal for source words. High-performing, but not low-performing, old and bilateral activity in prefrontal areas, a finding consistent with compensatory activations in old individuals.

The data on utilization and memory for context are relatively sparse in the imaging literature. Cabeza et al. (2002) yielded patterns of compensatory, bilateral activation in high-performing old adults for contextual retrieval relative to young individuals, but the Otsuka et al. (2001) study, which focused on encoding, did not show a compensatory pattern and found decreased activation primarily in ventromedial temporal areas. Close to other studies are needed in the imaging literature on aging.

individual Differences and Memory

Cognitive aging researchers have frequently used individual differences in various characteristics among subjects to explain sources of variance in memory function. For example, Lindsborger and Baltes (1994) and Baltes and Lindsborger (1997) reported that individual differences in sensory function (audition and vision) mediated substantial variance on a long-term memory task. Park et al. (1996, 2002) found that individual differences in speed and working memory accounted for age-related variance on many types of long-term memory tasks, including free recall, cued recall, and spatial recall. The importance of education and social context in response to environmental support has also been studied (Craik, Byrd, & Swanson, 1987; Cherry & Park, 1993). Work has even demonstrated that individuals' variability in performance on free-recall tasks over days may be an important predictor of later cognitive decline (Hultsch et al., 2000; Li et al., 2001).

Although the data on individual differences as predictors of patterns of neural function associated with memory are limited, the study of individual differences is a very powerful technique for understanding conflicting findings across studies. Characterizing subjects through neurophysiological batteries may provide substantial insight into the functional significance of different activation patterns. To the extent that bilateral patterns of activation are associated with good performance, it would suggest that recruitment of two hemispheres is likely compensatory for declining neural efficiency (Cabeza, 2002; Cabeza et al., 2002; Fozard et al., 2002).

On the other hand, if memory performance is poorer in individuals showing bilateral patterns of activation, the meaning of the pattern becomes somewhat harder to interpret. It may be that only low-memory subjects show bilateral recruitment patterns because only these subjects need the additional neural resources to perform the task (see the Daselaar and Cabeza walking stick argument in chapter 14 of this volume). At the same time, perhaps poor subjects are more diminished or increased activation is a marker of cognitive dysfunction. Note that the data presented in figure 1 of Lustig et al.'s 2003 work could support either argument.

At this time, there are six studies (Cabeza et al., 2002; Reuter et al., 2002; Logan et al., 2002; Lustig et al., 2003; Stabins et al., 2002; Dzemaliar, Velmans, Rombeau, Laizeron, & et al. 2003) relating individual differences in cognitive performance to patterns of neural activation. Of these, two suggested that bilateral activation patterns are associated with good performance, the other four reached the opposite conclusion. Cabeza et al. (2002) examined low- and high-memory subjects based on a battery developed by Gilkey, Polter, and Routelcan (1995). They imaged source retrieval using PET and reported that high-functioning old adults showed bilateral, but that lower functioning old individuals exhibited changes in activation within sites in a single hemisphere. Cabeza et al. argued that lateralization recruitment in

at encoding and the support that context may provide at retrieval. Neuroimag- ing studies have the potential to provide great insight into strategy differences at encoding and context utilization differences between young and old adults at both encoding and retrieval.
older adults is reflective of neural modification and reorganization over time to compensate for declining structural integrity of the nervous system. In support of this finding, Rosen et al. (2002) also reported that older subjects who scored highly on a memory battery outside the scanner showed not only the typical left prefrontal activation pattern, but also greater right prefrontal activation than young adults. In contrast, low-performing elderly showed reduced activations in both left and right frontal regions.

These findings are generally supportive of a compensation view (Cabeza, Grady, et al., 1997; Cabeza, 2000, 2002; Cabeza, 2002). Unfortunately, other studies that have related individual differences in performance to patterns of neural activation yielded the opposite conclusion, that is, that bilaterality is more characteristic of poorer performers. Logan et al. (2002) reported that bilaterality of the frontal cortex across a number of different encoding conditions was most likely to be evidenced by the oldest adults, whereas young adults and the younger subset of older adults showed a more selective (unilateral) recruitment pattern.

In a follow-up study, Lustig et al. (2003) considered healthy old and old adults in early stages of Alzheimer’s disease. As displayed in figure 9.1a, both groups showed increased left frontal activation during encoding of words, suggesting increased activation in this area was characteristic of aging. More important for the present issue, however, is that there were differences between the healthy elderly and patients with early Alzheimer’s disease in the medial parietal/posterior cingulate cortex (figure 9.1b). In this area, patients with Alzheimer’s disease displayed more activation during encoding than healthy elderly, and healthy elderly exhibited more activation than young adults. This pattern of findings is strongly suggestive of increased activation as dysfunctional, although note that these activations were outside the perifrontal cortex. Perhaps activations in some frontal areas are compensatory for old individuals, and other areas are dysfunctional. We recognize, of course, that the argument cannot be ruled out that additional recruitment, such as that displayed in figure 9.1b, occurs because of its compensatory value for neural deterioration in patients with Alzheimer’s disease.

Also reporting evidence of increased activation in poor performers, Stuss et al. (2002) found that decreased performance on neuropsychological tests was correlated with decreased frontal lobe activation on a deep-encoding task, and that bilaterality in adults reduced from left hemisphere activation rather than increased right hemisphere activation.

Finally, Daseela, Veltman, Rombouts, Latzeron, et al. (2003), using an incidental deep-encoding task focused on face-name associations, subjects into old and young individuals showed greater medial temporal activations than old and young adults and relatively equivalent activation and lateralization of frontal activity. At retrieval, old adult males exhibited widespread greater activation, although these differences vanished when only correct responses were included in the analysis.

How can these findings be reconciled? There is no apparent consistent threat to manipulations used in these studies. Of the four studies reporting evidence that high activation or bilaterality is characteristic of poor performers (Daseela, Veltman, Rombouts, Latzeron, et al., 2003; Logan et al., 2002, Lustig et al., 2003; Stuss et al., 2002), all used deep-encoding tasks, but so did a study finding evidence for compensatory bilaterality (Rosen et al., 2002). The relationship of encoding and retrieval operations is also unclear because compensation was found in one encoding and one retrieval study even though all four studies that found evidence for dysfunctional increase of increased recruitment studied encoding.

What is clear is that heightened activation in frontal areas relative to young individuals is significant for understanding the cognitive neuroscience of aging, and that there are conditions under which the activation is functional and others for which it is dysfunctional. It seems likely that carefully characterizing large numbers of subjects on multiple imaging and behavioral memory tasks, as well as relating performance to other domains of cognition such as language and visuospatial skills, will provide tremendous insight into these provocative and important relationships.

Conclusions

At the end of each section of this chapter, we summarized findings and recommendations for future research in particular domains. We now adopt a broader view and conclude by addressing two issues. First, how consistent are current behavioral theories of memory with extant neuroimaging data? Second, how do neuroimaging findings and theories change our view of memory function with age?

Theories of Aging and Memory

Cognitive aging theories of memory are typically based on single-mechanisms constructs, and the complexity of neuroimaging data does not readily map onto these theories. Nevertheless, some behavioral constructs and mechanisms are more sensibly instantiated in the imaging literature than others. Theories of resource, such as views that suggest that decreases in speed of processing account for declines in fluid cognition with age (Salihouse, 1996), cannot account for the patterns of neural activation that occur with declines in memory performance in older adults. At present, the proposed causes of declines in speed with age are decreases in white matter integrity, dopamine receptors, neocortical thickness, and demyelination of axons (see Park et al., 2001, for a review). To support a view that speed changes are causal for age-related cognitive decline, it would be important to directly link decreased speed to these specific changes in the brain and then map these changes to memory function. This is an obvious and a salient and at this stage of development in the imaging literature, more proximal linkages between mechanisms and neural activations may be established more readily.
cause that trace is less affected by aging than recollection. Findings of hippocampal/ prefrontal distinctions in memory processes are also reminiscent of Jacoby’s theory, with medial temporal activations reflecting automatic judgments of memory, and prefrontal activations indicating effortful strategic memory processes (Moscovitch & Winocur, 1992). Such a view would seem to suggest that older adults have less prefrontal involvement in retrieving memories, showing overall lower levels of activation in this area, and conceivably relying more strongly on hippocampal activations. Although the findings in the present review have been largely suggestive of decreased hippocampal function with age, Maguire and Frith’s (2003) finding that older adults had greater hippocampal engagement for stimuli associated with their personal lives would seem to support the view that older adults rely more strongly on familiarity in making memory judgments.

Neuroimaging Findings and Memory Theories

We now question how neuroimaging findings are changing theories of memory. At present, we would argue that neuroimaging findings are used as confirmatory data for extant behaviorally based theories of memory. That is, as behavioral theories are proposed, elaborated, and revised, they now must be able to accommodate neuroimaging findings because a failure to do so would indicate an inadequate theory or framework. At the same time that behavioral theories are evolving to accommodate neuroimaging findings, we also see evidence that particular interest is directed toward developing theories of memory plasticity and change in late adulthood, and we are seeing increased interest as well in interventions to improve memory and neural function (Logan et al., 2002). Memory theories are under development based on notions of compensation (Cabeza, 2002).

Given this new extraordinary ability to measure change and remodeling of neural organization with age that has resulted from imaging tools, we expect that theories of memory will increasingly be revised to integrate mechanisms of change or improvement in function in late adulthood as a result of training, contextual manipulations, or stimulation. Even from the relatively sparse and contradictory literature presented in this review, it is abundantly clear that the relatively static decline functions that occur in long-term memory across the life span are not mirrored in a pattern of linear decline in neural activation across an array of brain structures thought to be associated with memory.

Neuroimaging findings have also reinvigorated research that addresses hypotheses suggesting memory function can be broadly trained (Kramer & Willis, 2002), that cognitive vitality can be enhanced through exercise (Colcombe & Kramer, 2003), and that cognitive and social engagement facilitate a healthy mind (Schoolder & Malina, 2001). Because tools are at last available that provide sensitive measurement of neural function, we believe that studies of patient groups with affected memory function (e.g., from Alzheimer’s disease, Parkinson’s disease) will provide new insight into models of normal memory function in late adulthood.

Finally, we are convinced that the complex patterns of findings in the neuroimaging literature can only be understood through the study of individual differences along with studies that systematically manipulate variables that increase or decrease
difficulty of encoding in a systematic fashion. This will permit subjects to be categorized according to behavioral patterns of function (e.g., Gilkey, Poliner, & Rothi-
cox's 1995 bar test) for characterizing subjects in terms of frstal and hipposcampal function) as well as neural patterns, such as bilateralizer (Cabeza, 2002) or decreased neural selectivity (Logan et al., 2002; Pirk et al., in press).

Despite the many concerns we have expressed regarding interpretation of results from the neuromaging techniques have provided remarkable accuracy and validation for the study of aging and memory. Memory func-
tors have fnt new ideas for development and measurement of conceptual models. We predict that cognitive neuroscience will be the dominant perspective from which theories of aging and memory evolve over the next decade.

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